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RESEARCH PAPER

Diet and locomotion, but not body size, differentiate mammal communities in worldwide
tropical ecosystems

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22 **ABSTRACT**

23

24 **Aim**

25 To test whether tropical habitat groups across the world can be differentiated by using
26 taxon-free mammalian community structures and to discuss the implications of this
27 analysis for palaeoecological community studies.

28

29 **Materials and Methods**

30 We used mammalian community data for 169 localities, which were assigned *a priori* to
31 hierarchical Olson (1983) vegetation categories. Species over 500 g were classified into
32 dietary, locomotion, and body mass groups and the resulting group structures were
33 analysed using community structure analyses (NPMANOVA, CAP, SIMPER).

34

35 **Results**

36 The test results show that the mammalian community structures are significantly different
37 between all of Olson's categories. These differences are highest at Olson's major and
38 minor ecosystem levels, and require the least number of variable categories. At the
39 vegetation level, the number of variable categories required to distinguish between them
40 becomes higher. Of the dietary groups, the number of frugivore-granivores, frugivore-
41 omnivores, grazers and mixed feeders contribute most to these differences, while the
42 number of arboreal, arboreal-terrestrial and subterranean-terrestrial species are the key
43 locomotor groups. Body mass was not a good discriminator.

44

45 **Main conclusions**

46 As general ecosystem categories are broken down into more precisely defined habitats, it

requires more detailed knowledge of the species adaptations to distinguish between them. Many of Olson's vegetation groups represent a continuum of cover that are, at least at the worldwide comparison, too detailed to differentiate when broad generalities are sought. We suggest using three worldwide tropical major ecosystems in mammalian community structure analyses: "Humid, closed forests", "Seasonal or interrupted forests and grasslands", and "Seasonal, open drylands". Our results also demonstrate that community structures defined by both dietary and locomotor adaptations are powerful discriminators of tropical ecosystems and habitats across the continents we examined, but body mass should be interpreted with caution when the research question pertains to multiple continents.

1. INTRODUCTION

The use of mammalian communities as proxies for past habitats and environmental conditions has a long established history (e.g. Andrews *et al.*, 1979). Such synecological studies may employ a taxonomic approach in which communities with similar taxonomic compositions are considered to have inhabited analogous environments (Simpson, 1943; Fleming, 1973). However, a “taxon-free” approach is favoured by palaeoecologists concerned about the difficulties in identifying species in the fossil record and the assumption that fossil taxa behaved the same as their modern forms (Harrison, 1962; Andrews *et al.*, 1979; Andrews and Hixson, 2014). Such studies focus on how the resident species exploit available spatial and trophic niches irrespective of taxonomic identity through an evaluation of each taxon’s adaptations to specific ecological variables, including dietary preferences and locomotor patterns.

Freed from the need to identify specific taxa, communities from different continents and time periods can be compared, giving us the tools to analyse past environmental changes, palaeoclimates and habitat distribution on a global scale. However, many mammalian community studies are restricted to a single geographical realm (e.g. Andrews *et al.*, 1979; Reed, 1997, 1998; Mendoza *et al.*, 2004), with few concentrating specifically on mammalian communities between continents (e.g. Kelt *et al.*, 1996; Andrews & Humphrey, 1999; Rodríguez *et al.*, 2006). An implicit assumption in these studies is that mammalian communities from the same types of environment will have similar community structures between continents.

98 Comparisons of communities from different world regions can reveal global generalities,
99 assuming that the relationship between size and abundance of species within specific
100 geographical locations and habitats tells us something about the partitioning of resources
101 in natural communities (Peters & Raelson, 1984; Fa and Purvis, 1997). For example, the
102 distribution of species in various classes of body sizes, feeding adaptations, and food
103 habits suggest that the structure of Old and New World tropical mammalian communities is
104 very similar (Fleming, 1973). However, other research demonstrates that despite general
105 resemblances communities from regions with similar climates can radically differ in certain
106 features (Dubost, 1984; Fleagle and Reed, 1996; Fa and Purvis 1997; Rodríguez *et al.*,
107 2006), possibly relating to historic effects. Ecosystems evolve over time (Olson, 1966;
108 Andrews *et al.*, 1979; Janis 1993); tectonic, regional, historical and climatic processes may
109 all play a role. Mountain uplift (e.g. the rainshadow cast by the uplift of the East African rift;
110 blocking of the monsoonal winds to Central Asia by uplift of Himalayas), changes in
111 oceanic circulation (opening of Drake's passage between Antarctica and Australia,
112 resulting in a cold circumpolar current around Antarctica), closing of the Tethys sea in Late
113 Miocene to form the Mediterranean, isolation (e.g. Australia with its unique fauna),
114 interchange between continents (e.g. the Great American Interchange of the late Pliocene)
115 and major ecosystem changes (e.g. the current arid configuration of Sahara at the end of
116 the Holocene climatic optimum) each contribute to differences between regional species
117 pools and vegetation (Janis 1993; De Vivo and Carmignotto 2004; Louys *et al.*, 2011;
118 Fortelius 2013; Owen-Smith 2013). This presents a challenge in distinguishing between
119 historical and ecological factors in community structure (Endler 1982) and likewise
120 suggests that mammal community structures around the world will present some
121 significant differences.

122

In light of this, we analyse modern mammalian community structures across the tropical belt of four continents: the Americas, Africa, Asia and Australia, which is frequently neglected. We address the following question: can tropical habitats across the world be differentiated on the basis of their mammalian community structures?

2. METHODS

2.1. Localities

This study includes 169 extant tropical localities between 23° 30 N and 23° 30 S (Fig. 1, Appendix S1 in Supporting Information) from previously published studies including Andrews, *et al* (1979) (n= 23), Andrews & Humphrey (1999) (n=16), Reed (1997) (n=18) and Reed (2008) (n=8) and the database compiled by the National Center for Ecological Analysis and Synthesis (NCEAS) workshop on Mammalian Communities (see Badgley *et al.* 2001; van Dam *et al.* 2001; Damuth *et al.* 2002) (n=100). This is supplemented by four unpublished localities from P. Andrews (n=3) and K. Reed (n=1). We endeavoured to use only communities comprised of more than 20 species to ensure completeness of the locality species lists, although in some cases (i.e. tundra and montaneous habitats) the number is naturally not likely to be this high (Appendix S1).

Coordinates for each locality were taken from Andrews *et al.* (1979), Andrews & Humphrey

(1999), the NCEAS database and WDPA, the World Database on Protected Areas (IUCN and UNEP 2009). Site-specific references were also consulted (Appendix S1).

2.2. Vegetation categories

We used the vegetation classification system of the “Major World Ecosystem Complexes Ranked by Carbon in Live Vegetation” GIS dataset, which characterises the vegetative cover of the Earth's land surface in 0.5 by 0.5 degree grid cells (Olson *et al.*, 1983, 1985). The classes can be applied across continents because the system explicitly uses natural vegetation categories without defaulting to generalised physiognomic categories or specific vegetation types (i.e. coconut groves) like those considered in other systems (White, 1983; Eiten, 1992; Lawesson, 1994).

Olson *et al.* (1983) organises vegetation categories into a hierarchical structure with six levels of increasing complexity. Our analyses are conducted at three different levels corresponding to Olson *et al.*'s (1983) third, fourth and sixth. Their third level, which describes the landscape, is a broad grouping which we call ‘*major ecosystems*’. The fourth we call ‘*minor ecosystems*’, which takes into account latitudinal and altitudinal effects. Their sixth level takes into account temperature, moisture and seasonality. For this we use the term ‘*vegetation category*’ (Table 1). We excluded seven categories associated with human impact and agriculture (Leemans *et al.*, 1996) and 11 marginal categories that did not describe our localities. Detailed descriptions of selected categories are found in Olson *et al.* (1983).

Localities may cover tens or thousands of kilometres of space depending on whether they

are national parks, small conservancies, etc. This is not unlike other community analyses (e.g. Reed, 1998; Mendoza *et al.*, 2004). Although one can expect there to be some variation in topography and vegetation on the ground, especially where larger localities are concerned, our samples were selected for their relative homogeneity. Each locality was assigned to a vegetation category by comparing the detailed descriptions in our primary sources to those of Olson's to further ensure that we were correct in our interpretation and that each of the localities did not include multiple broad vegetation complexes. The comparison was first made against the vegetation groups within the same grid cells where the localities are situated, then against the neighbouring ones, followed by those applicable to the tropical region of the locality's country and finally for the whole country. The number of localities included in each vegetation category is summarised in Table 2.

2.3. Locality species lists

Species lists for each locality are derived from the published literature (Appendix S1; S2). We only consider species weighing more than 500g (n=607), as micromammals may be under-sampled in modern studies and are poorly represented in fossil sites. We restrict our analysis to non-volant mammals and exclude Chiroptera, Sirenia and Cetacea. This follows a well-established practice of excluding these groups in palaeoecommunity analyses due to the practical difficulties with including them as fossil species; they do not frequently fossilise or they are fossilised under very different taphonomic conditions compared to other, land-dwelling- or larger mammals. Given this, and their rarity in the fossil record, most workers thus exclude them (e.g. Andrews *et al.*, 1979; Reed, 1998; Kovarovic *et al.*, 2002; Mendoza *et al.*, 2004; Louys *et al.*, 2011). All of the species were matched against the taxonomy of Wilson and Reeder (2005).

2.4. Ecological variables

We assigned species to categories in four ecological variables: body mass, locomotor pattern, and two hierarchical dietary categories. These data are from NCEAS (Badgley *et al.*, 2001; van Dam *et al.*, 2001; Damuth *et al.*, 2002), PanTHERIA (Jones *et al.* 2007) and MammalBase (Liow *et al.*, 2008; Liow *et al.*, 2009; Lintulaakso, 2013), a compilation of species attributes and diets based on hundreds of published sources.

2.4.1. Body mass

Taxa were assigned to a body mass category based on median body weights from several published sources (Appendix S2). Mass categories are modified from those in Andrews *et al.* (1979): 0.5-8 kg (A), 8-45 kg (B), 45-90 kg (C), 90-180 kg (D), 180-360 kg (E), and 360+ kg (F).

2.4.2. Locomotion

We divided the species into six locomotor groups which describe the substrate(s) in which the species moves (Reed, 1998; Miljutin, 2009): arboreal (A), arboreal-terrestrial (AT), subterranean (S), subterranean-terrestrial (ST), terrestrial (T) and terrestrial-aquatic (TA). If a species was found in several different references, the most common locomotion group among these was used (Appendix S2).

2.4.3. Diet

The dietary variable is divided into two levels of food resource preference (Table 3). Diet Level 1 represents the broadest categories of feeding strategy: animalivorous, frugivorous and herbivorous (Miljutin, 2009). Diet Level 2 follows that of Eisenberg (1981) with some modifications: mixed-feeders are added to the herbivore group, and aerial insectivores and foliage-gleaning insectivores are combined into one category: insectivores. As with locomotion, where a species was described in multiple references, the mostly frequently cited dietary preference was used (Appendix S2).

2.5. Analysis

Community structure data may be summarised in two ways: as raw counts of species in each category at each locality or converted to a percentage of the total number of species at each locality. Percentage data is common (Harrison, 1962; Fleming, 1973; Andrews *et al.*, 1979; Reed 1997, 1998; Kovarovic *et al.*, 2002; Louys, 2007; Louys *et al.*, 2009; 2011), raw count data much less so (Mendoza *et al.*, 2004, 2005; Rodríguez *et al.*, 2006). However, the use of percentages is potentially problematic because they generate a closed system (Aitchison 1986; Hernández & Vrba, 2006), giving rise to the so called 'closure problem' (Butler, 1981) in which the variables lack statistical independence (Jackson, 1997). It is most noticeable with few variables and decreases in magnitude as the number of variables is increased (Grayson, 1984; Jackson, 1997). As some of our analyses had only three groups, we use the number of species within each group transformed to $\log_2(x) + 1$ for $x > 0$, where x is the number of species (Anderson *et al.*, 2006; decostand in R package vegan (Oksanen *et al.*, 2007)). After transformation, a

247 Bray–Curtis distance matrix was calculated (Bray & Curtis, 1957; Legendre & Legendre,
248 1998). Analyses were conducted in R 3.0.0, using R-packages *stats* and *vegan* (Oksanen
249 *et al.*, 2007; R Development Core Team, 2005).

250

251 We tested spatial autocorrelation using the Mantel test (Mantel, 1967). Mantel r of
252 association between Bray-Curtis dissimilarity and distance among sites ranged from a
253 moderate of 0.43 (Mass) to a low of 0.16 (Locomotion) with randomization P-value of
254 0.001 (999 permutations, results not shown). Mantel correlograms showed that spatial
255 correlation is highest in 414, 1243, 2072, and 2901 km class indices, i.e. localities which
256 are closer together (within a continent) did tend to have more similar species composition.
257 However, both CAP and NPMANOVA (see below) are non-parametric tests and, as such,
258 are not affected by autocorrelation. If the observations are correlated with one another
259 (e.g., temporally or spatially), then randomly shuffling them will eliminate this inherent
260 structure, if it is present (Anderson, 2005). Therefore, a sensitivity analysis was performed
261 using the original Bray-Curtis distance and the distance between NMDS space. The results
262 were visualized with a Shepard plot (not shown here). For two axes ($k=2$), the resulting
263 stress values were 0.09, 0.11, 0.12, and 0.15 for body mass, locomotion, diet level 1, and
264 diet level 2 respectively. Values <0.1 correspond to a good ordination and values <0.2 still
265 provide useful 2-dimensional ordination of the data (Clarke and Warwick, 2001).

266

267 We performed a constrained ordination (CAP, Canonical Analysis of Principal Coordinates;
268 Anderson and Willis, 2003) to determine if there are differences among mammalian
269 communities. CAP finds the canonical axis that best separates groups in multivariate
270 space, and it also tests the hypothesis of no significant differences in multivariate location
271 among groups. We plotted the product-moment correlation coefficient for each ecological

variable value with each of the canonical axes. High absolute correlation is interpreted as an important factor for the nature of group differences (Anderson and Willis, 2003). A non-parametric *a priori* test for differences among groups was also conducted using the permutational multivariate analysis of variance (PERMANOVA or NPMANOVA; Anderson, 2001), followed by SIMPER (similarity percentage) which determines the relative contribution of each ecological variable to the dissimilarity between groups (Clarke, 1993). If a specific variable consistently contributes to both the within-group similarity and between group dissimilarity, it is considered a good discriminator.

3. RESULTS

3.1. General analyses

Both the NPMANOVA and CAP test results show that the mammalian community structures are significantly different between all categories (NPMANOVA , $p < 0.001$, CAP, $P = 0.005$ Tables 4 & 5).

3.2. Ecological variable analyses

3.2.1. Diet

Most of the communities are significantly different between major ecosystems at both dietary levels (NPMANOVA). In the CAP analysis, the number of frugivorous (mainly frugivore-granivores and frugivore-omnivores) and herbivorous (grazer and mixed feeder)

species contribute most to the constrained ordination between major ecosystems (Fig. 2a). SIMPER results indicate that the number of frugivorous species is important at Diet Level 1, and at Diet Level 2 frugivore-granivores contribute most to the dissimilarities between major ecosystem communities. As Olson's categories become more specific (i.e. major ecosystem to minor ecosystem to vegetation category), the number of dietary categories required to distinguish between them becomes higher (Table 6).

3.2.2. *Locomotion*

Between most of the category pairs, the mammalian community structures are significantly different (NPMANOVA). In the CAP analyses, the number of arboreal, arboreal-terrestrial and subterranean-terrestrial species contribute most to the differences (Fig. 2b). SIMPER results indicate that the number of arboreal or arboreal-terrestrial species is important for the dissimilarities between communities; the subterranean-terrestrial, terrestrial-aquatic, and terrestrial species contributed much less so (Table 7)

3.2.3. *Mass categories*

In NPMANOVA body mass categories were not as dissimilar between mammalian groups as the other variables. CAP shows that the number of small species contributes most to the group differences (Fig. 2c). In SIMPER, the number of large (360+ kg) and small (0.5-8 kg; 8-45 kg) species has the highest contribution to the dissimilarities between category pairs (Table 7).

3.3. Mammalian community structures in Olson's categories

3.3.1. *Major forest and woodland (FW) and sub-categories within it*

FW differs from the other major ecosystems; the only exception is “major wetlands” (WL). It has the largest number of frugivorous and arboreal species compared with more open ecosystems “grass and shrub complexes” (GS) and “tundra and desert” (TD). SIMPER indicates that the lower number of herbivorous species in FW and the lower number of arboreal species in “interrupted woods” (IW) distinguish these two ecosystems.

At the minor ecosystem level, the “main tropical/subtropical forest” (TSF) had similar results as FW. The “mid-latitude broad-leaved and mixed forest” (MBF) differed from the IW ecosystems by having lower number of subterranean-terrestrial species. MBF had also fewer terrestrial species than “main grassland or shrubland” (MGS), and more arboreal-terrestrial species than “nonpolar desert or semidesert” (SDS).

At the vegetation level, TSF has three sub-groups. These groups are dissimilar between each other and most of the other vegetation groups. However, there were no significant differences between the “tropical dry forest and woodland” (RGD) vs. “tropical savanna and woodlands” (SGW) and “tropical/subtropical broad-leaved humid forest” (TBS) vs. “Tropical montane complexes” (TMC) pairs (Tables 6, 7).

3.3.2. *Interrupted Woods (IW) and sub-categories within it*

IW differed from the other major ecosystems, WL being the only exception. However, at the minor ecosystem level, the “other dry woods mosaics” (DWM) could be differentiated from the wetlands by having fewer arboreal species.

At the vegetation level, there were no significant differences between SGW and the “warm or hot shrub and grassland” (MGS) nor between the SGW and RGD as mentioned earlier (Tables 6, 7).

3.3.3. *Grass and Shrub complexes (GS)*

This major ecosystem had only one minor ecosystem and vegetation group, MGS. GS differs from the other major ecosystems at some of the four community variables. At the minor ecosystem level, MGS did not differ from “nonpolar desert or semidesert” (SDS) and, at the vegetation level, MGS was not different from “tropical savanna and woodlands” (SGW) or “desert and semidesert, (no winter snow)” (SDS) (Tables 6, 7).

3.3.4. *Tundra and Desert (TD) and sub-categories within it*

TD differs from the other major ecosystems. It had the least number of species in all of the community variables. TD is divided into two minor ecosystems, SDS and “tundra, arctic desert and ice” (TUN¹), but they do not differ. As mentioned above, MGS and SDS were similar with each other, but MGS and TUN were not (Tables 6, 7).

3.3.5. *Major Wetlands (WL)*

¹ The only localities from TUN were high Alpine tundra localities from South America.

371

372 This major ecosystem had only one vegetation category, “warm or hot wetlands,
373 swamp/marsh” (SWP). WL is the only major ecosystem that does not differ from FW and
374 IW. At the vegetation level, it can only be differentiated from forested (TBS, TRF) or open
375 habitats (SDS, TUN) (Tables 6, 7).

376

377 4. **DISCUSSION**

378

379 We tested whether tropical habitats across the world can be differentiated on the basis of
380 their mammalian community structures. Generally, our results show that the diet and
381 locomotion categories differentiate the communities best, while body mass performed
382 poorly. As Olson’s categories become more tightly defined, the number of ecological
383 variable groups required for differentiation becomes higher. Differences between treeless
384 categories, such as desert and grasslands, are not significant.

385

386 4.1. **Ecological variables**

387

388 Differences noted between dietary categories are largely accounted for by the number of
389 frugivores. At Diet Level 2, this signal comes from frugivore-granivores (FG) and frugivore-
390 herbivores (FH) (but see ordination in CAP where frugivore-omnivores are also important,
391 Fig. 2a). Many of these species are primates but there are other frugivorous groups, such
392 as ungulates, also present in high numbers in tropical forests which are under-represented
393 in open habitats such as savannas and grasslands (Bodmer, 1990).

394

395 Others have found that the separation of vegetation groups relates more to the

396 grazer/browser continuum, rather than the abundance of frugivores (Sponheimer *et al.*,
 397 1999; Janis *et al.*, 2000). In our study, the number of herbivores (mainly grazers and
 398 browsers in SIMPER, grazers and mixed-feeders in the CAP ordination) is important only
 399 at the minor ecosystem and vegetation level where “interrupted woods” (IW) and treeless
 400 areas like grasslands and tundra, are differentiated from each other. Animalivorous groups
 401 do not impact on the differences between major or minor ecosystems but, at the vegetation
 402 level, the low number of carnivorous species in MGS distinguishes this habitat from RGD.
 403 Similar results were obtained by Reed (1997, 1998) where frugivores, fruit/insect eaters
 404 and grazers discriminated between habitats with no clear contribution from animalivorous
 405 taxa. Herbivores and frugivores are mainly primary or secondary consumers while
 406 animalivores are higher in the trophic hierarchy. This may be the reason why habitats are
 407 reflected more by their primary and secondary consumers and the ‘signal’ from the primary
 408 production weakens towards the top of the trophic hierarchy.

409

410 When we compare results between Diet Level 1 and 2, the differentiation of the major and
 411 minor ecosystems and the vegetation categories is based on similar variables which relate
 412 to the abundance of frugivores and herbivores. The differences are more nuanced when
 413 we consider Diet Level 2, with between one and six variables required to distinguish
 414 between various habitat pairs. The broader classification (i.e. Diet Level 1), requiring a
 415 consideration of only frugivory and herbivory, may make it a more robust approach for
 416 worldwide ecosystem and vegetation comparisons, although clearly less detail is captured.

417

418 In terms of the locomotion groups, the number of arboreally adapted species differentiates
 419 closed (FW, IW) from open habitats (GS, TD). This is a conclusion borne out by many
 420 others (Reed 1997; Louys *et al.*, 2011) who also demonstrate that an abundance of

421 arboreal species indicates the presence of well-developed tree cover. Primates and tree-
422 dwelling rodents comprise the majority of these taxa. The higher number of terrestrial-
423 aquatic species in wetlands (WL) only separated it from TD; otherwise WL did not
424 differentiate from FW and IW. We conjecture that the species lists from wetlands include
425 taxa from nearby areas that periodically visit for drinking and maybe counted as
426 inhabitants of both areas because they are observed in each. Interestingly, the number of
427 terrestrial species contributed very little to the differences between community structures in
428 SIMPER. Terrestriality may be too general of a category for describing species that move
429 about on the land surface. By adding more detailed locomotor classes (i.e. cursorial), the
430 separation between open and closed habitats could be clearer. In the CAP analysis, the
431 number of subterranean-terrestrial and terrestrial species did distinguish between humid
432 and forested localities (TBS, TRF) and seasonal or less forested areas (RGD, STW, SGW,
433 MGS). Seasonality and the inconsistent availability of food throughout the year can be
434 dealt with in two ways: migration, which requires terrestrial movement, or by caching food
435 resources, which subterranean-terrestrial species generally do.

436

437 Body mass categories did not clearly differentiate community structures, particularly in
438 vegetation categories. This may be a consequence of the scale of the investigation. Work
439 by Brown and Maurer (1989) has shown that the frequency distribution of body sizes
440 appears to be general; it is modal and skewed towards smaller species when large areas
441 (i.e. continents or biomes) are sampled, whereas there are approximately equal numbers
442 of species in each size category in smaller, local areas. They suggest that a strong
443 negative interaction prevents local coexistence of similar-sized species, so one would
444 therefore not expect that community structures could be distinguished at this scale.
445 However, further analysis of the data showed that the size ranges of mammals differed on

each continent. Africa has a higher proportion of larger mammals, whilst America and Australia have smaller species with Asia somewhere in between (Fig. 2d). This pattern is also observable in the palaeontological record of the Pleistocene and is likely to have roots deep in time (Janis 1993; De Vivo and Carmignotto 2004; Louys *et al.*, 2011; Fortelius 2013; Owen-Smith 2013).

We found that only the number of small (0.5-8 kg, 8-45 kg) and large (360+ kg) species has the highest contribution (SIMPER) for some of the community pairs. The importance of small species is likely that, as a group, there is more variety in both dietary preferences and locomotion. Large species are almost always terrestrial herbivores, separating grasslands and savannas from forests, whereas small species can be arboreal, terrestrial, subterranean, as well as insectivores, frugivores, and herbivores. Although a recent study (M. Rodríguez *et al.*, 2006) has shown that body size can be useful, this is only clear at higher latitudes suggesting that the warmer the annual temperature, the less likely body size is helpful in distinguishing habitats.

4.2. Distinguishing Olson's categories

Generally, major ecosystems can be differentiated by the dietary and locomotor adaptations of their constituent species, but body mass is not a robust discriminator. For example, mass does not differentiate the FW-IW-GS continuum. This is likely to relate to historical differences between the continents that have resulted in unique body size ranges that are not correlated with habitat (Louys *et al.*, 2011).

470 Minor ecosystems, particularly forested areas, are the easiest to distinguish from other
471 categories. However, some pairs share similar mammalian community structures. These
472 include MGS-SDS and SDS-TUN. Most of these are open environments that gradually
473 transform into each other across the landscape and are likely to share species that are
474 comfortably adapted to ecotones and a wider array of ecological conditions.

475

476 At the detailed level of vegetation category, the general pattern of differences between
477 forested and open areas are still noticeable: the number of frugivorous and arboreal
478 species account for most of the differences. However, the same types of pairs that did not
479 differentiate at the minor ecosystem level can now be distinguished. These include SGW-
480 RGD; SGW-MGS; TMC-TBS; MGS-SDS and SDS-TUN. The division of the minor
481 ecosystem TSM into SGW and TMC reveals the true nature of this group: SGW represents
482 more open and seasonal areas and TMC is more forested. This may be the reason why
483 SGW does not clearly differ from RGD and MGS. Both SGW and RGD have some number
484 of dry months during the year, are widespread and often mixed vegetation complexes
485 (Olson *et al.*, 1983). SGW is a mosaic that contains dry, grassy areas as well as places
486 that are similar to tropical seasonal forests. On the other hand, RGD may also alternate
487 with grassy savannas, so that points of separation become arbitrary (Olson *et al.*, 1983). In
488 the constrained ordination (CAP), RGD plotted near or within the SGW, STW, and MGS,
489 which indicates that seasonality plays a major role for the mammalian composition of this
490 vegetation group. TMC consists of rainy forests that may be locally denser than nearby
491 lowlands and are more similar to woodlands, such as RGD (Olson *et al.*, 1983). Other
492 studies have subsumed montane forests into a general forest category (e.g. Reed, 1998).
493 Although Olson classifies TMC as a part of interrupted woods (due to lower mean carbon
494 density), our results also suggest that the community structure of TMC is similar to forest

495 complexes and that it is not appropriate to consider this habitat a part of IW.

496

497 **4.3. Palaeoecological implications**

498

499 Our study confirms that palaeoecological reconstructions of tropical fossil localities based
500 on dietary and locomotor variables can be obtained. Questions raised regarding the
501 appropriateness of modern comparative datasets derived from localities across multiple
502 continents are possibly unwarranted, unless body size has been given significant
503 consideration. This is not to say that ecological differences between the continents do not
504 exist in the structure of communities. We showed some body mass differences with results
505 similar to others (e.g. Smith *et al.*, 2004; Louys *et al.*, 2011), particularly in demonstrating
506 that Africa has a higher number of large-bodied taxa; our tentative suggestion is that the
507 differences are perhaps more meaningful than other workers who emphasise that body
508 size distributions across continents are not significant (e.g. Smith *et al.*, 2004). . For
509 example, during the drier late Pleistocene last glacial maximum, the body mass groups of
510 mammalian faunas in South America and Africa were quite similar. However, during the
511 wetter Holocene climatic optimum there was a decrease in open vegetation areas that lead
512 to the loss of larger-sized mammal lineages in South America, whilst they survived in
513 Africa. As a result, today Africa is richer in the number of species above 5 kg (De Vivo and
514 Carmignotto 2004). In addition, Louys *et al.*, (2011) hypothesise that faunal exchange over
515 the past several million years between Africa and Asia contributes to community
516 convergence, whereas the much longer separation of the New World from the Old World
517 relates to differences between their communities. Furthermore, they posit that historical
518 factors function on a much longer temporal scale in shaping community structure, which

519 suggests that some caution is warranted in selecting comparative communities from
520 across the world for palaeoecological reconstructions of sites located on a continent that
521 has been long separated from the others, or for analyses involving deep time. This can be
522 interpreted from our results, too. Although we did not analyse continental differences in the
523 other ecovariables, our results show only relatively small numbers of similar mammalian
524 community structures within worldwide tropical vegetation classes. This indicates that
525 historical and ecological factors are shaping mammalian community structure slightly
526 differently in relatively similar primary production environments. (Endler 1982).

527 In addition to caveats regarding the usefulness of body mass as a habitat discriminator,
528 our results provide an additional principal observation for palaeoecological community
529 studies. Some vegetation groups represent a continuum of cover (TMC-TBS-TRF, RGD-
530 SGW-MGS-SDS) that are, at least at the worldwide comparison, too detailed to
531 differentiate when broad generalities are sought. This may be related to the methodology,
532 in which habitats on this continuum are forced into discrete categories for the sake of
533 analysis. The ecological reality is that differences between these groups are probably
534 much more subtle than these discrete categories can be analysed using our ordination-
535 based approaches and other common tests. One way around this problem may be to
536 focus on reconstructing not habitat categories specifically, but the variable amount of
537 canopy cover available in them, as Louys, *et al.*, 2015 have done. However, one may seek
538 more ecological detail than this, whereby the use of well-defined habitat categories is both
539 convenient and analytically manageable. Where this option is pursued, we suggest using
540 three worldwide tropical major ecosystems: “Humid, closed forests” that contains TMC,
541 TBS, and TRF; “Seasonal or interrupted forests and grasslands” that contains RGD, SGW,
542 and STW; and “Seasonal, open drylands” that contains MGS, SDS, and TUN (TBC and
543 SWP were difficult to differentiate from the other groups so they are excluded from our

three groups; the former exists mostly in mid-latitudes and is a marginal habitat in the Tropics, whilst the latter is a generalised category that can be found naturally within many other habitats). These broad groups are similar in structure to those described by Mendoza *et al.* (2004): “evergreen forests”, “wooded savannahs that share grass and browse” and “arid communities with sparse plant cover”. They identified these in strictly African communities, but they appear to hold at the global level, as well, further highlighting their utility in ecological reconstructions. Interestingly, these authors do not consider locomotion in their study, but assign each large mammal taxon to a group which combines feeding strategy and body size.

The data as we have analysed them herein demonstrate their wide applicability in distinguishing between modern habitats and, by extension, fossil localities where relatively complete species lists can be obtained. We appreciate that defining palaeospecies is not a straightforward task, but since we find that more precise habitat reconstructions are every bit as possible as broad ecosystem discrimination where increasingly detailed species information is analysed, palaeontological research should continue to approach questions of individual species adaptive complexes, as well as palaeocommunity structures and habitat affiliations.

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754

755 BIOSKETCH

756

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764

765 SUPPORTING INFORMATION

766 Additional Supporting Information may be found in the online version of this article:

767 **Appendix S1:** 169 localities from within the tropical belt

768 **Appendix S2:** Locality species and ecological variable assignments